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Citation for final published version:

Boscolo-Galazzo, Flavia ORCID: <https://orcid.org/0000-0002-5146-5321>, Crichton, Katherine A., Barker, Stephen ORCID: <https://orcid.org/0000-0001-7870-6431> and Pearson, Paul N. ORCID: <https://orcid.org/0000-0003-4628-9818> 2018. Temperature dependency of metabolic rates in the upper ocean: A positive feedback to global climate change? Global and Planetary Change 170 , pp. 201-212. 10.1016/j.gloplacha.2018.08.017 file

Publishers page: <http://dx.doi.org/10.1016/j.gloplacha.2018.08.017>
<<http://dx.doi.org/10.1016/j.gloplacha.2018.08.017>>

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Temperature dependency of metabolic rates in the upper ocean: A positive feedback to global climate change?

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ARTICLE INFO

Keywords:

Metabolic theory of Ecology
Temperature dependency
Biological pump
Carbon cycle
Climate change

ABSTRACT

The temperature of seawater can affect marine plankton in various ways, including by affecting rates of metabolic processes. This can change the way carbon and nutrients are fixed and recycled and hence the chemical and biological profile of the water column. A variety of feedbacks on global climate are possible, especially by altering patterns of uptake and return of carbon dioxide to the atmosphere. Here we summarize and synthesize recent studies in the field of ecology, oceanography and ocean carbon cycling pertaining to possible feedbacks involving metabolic processes. By altering the rates of cellular growth and respiration, temperature-dependency may affect nutrient uptake and food demand in plankton and ultimately the equilibrium of pelagic food webs, with cascade effects on the flux of organic carbon between the upper and inner ocean (the “biological carbon pump”) and the global carbon cycle. Insights from modern ecology can be applied to investigate how temperature-dependent changes in ocean biogeochemical cycling over thousands to millions of years may have shaped the long-term evolution of Earth's climate and life. Investigating temperature-dependency over geological time scales, including through globally warm and cold climate states, can help to identify processes that are relevant for a variety of future scenarios.

1. Introduction

Almost all chemical reactions go faster at higher temperature, including biologically mediated reactions within cells (Cossins and Bowler, 1987). However, the extent to which a given reaction is temperature-dependent is quite variable and depends in part on its activation energy. For instance photosynthesis and respiration, two of the most fundamentally important metabolic processes on a global scale, respond very differently to ambient temperature (Brown et al., 2004; Allen et al., 2005; Chen et al., 2012). All other factors being equal, an increase in temperature strongly favours respiration and hence the remineralization of organic carbon back to CO₂. Because the planet as a whole can experience substantial changes in surface temperature, a series of cascading feedbacks could, in principle, occur, involving both terrestrial and marine carbon cycling.

The ocean represents a major sink for atmospheric carbon, partly through the “biological carbon pump” in which sinking organic matter is exported from the surface to the deep sea (Passow and Carlson, 2012). The efficiency of the pump relies on a fine balance between the counteracting metabolic processes of carbon fixation into organic matter by photosynthesis and remineralization back to CO₂ by

respiration (Passow and Carlson, 2012). When organic carbon is moved to the deep ocean and/or buried, it creates a return flux from the atmosphere to the surface ocean. As the global ocean changes temperature, the balance between the two processes is likely to shift. If global temperatures increase, the efficiency of the ocean as a carbon sink should decline, and vice versa in a cooling world. This is potentially a very important positive feedback on global climate and atmospheric CO₂ levels.

In recent years an increasing number of studies have addressed various aspects of this potential climate feedback, both from the point of view of modern processes and likely future climate, and also the paleoclimate record. Despite that, the subject received little attention in the most recent Scientific Assessments of the Intergovernmental Panel on Climate Change (IPCC, 2013).

In this article we consider the issue from an ocean perspective, focusing on physiological processes in the plankton that may affect the partitioning of carbon between the atmosphere, surface ocean and deep ocean. Exploring these biological mechanisms in the present and the past can progress our understanding of climatic and CO₂ changes through the Cenozoic and potentially provide clues about the future. Investigating how subtle physiological mechanisms and climate interact

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<https://doi.org/10.1016/j.gloplacha.2018.08.017>

Received 27 March 2018; Received in revised form 28 August 2018; Accepted 28 August 2018

Available online 30 August 2018

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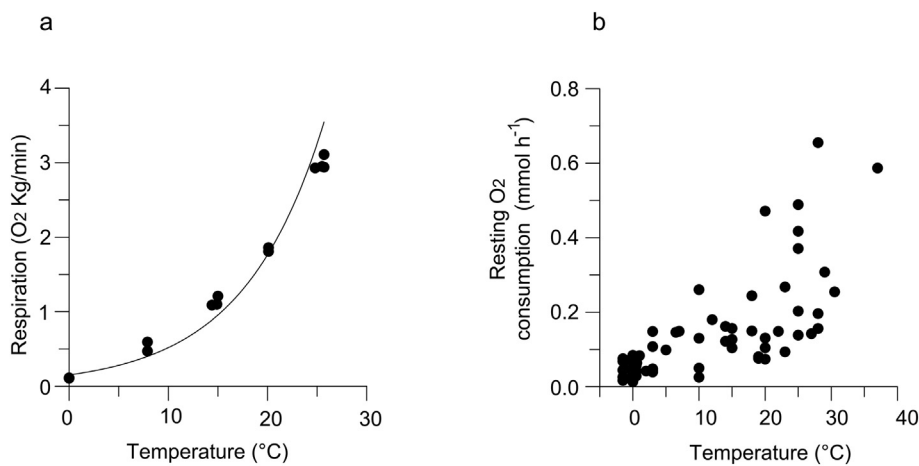


Fig. 1. Relation of resting metabolic rate to temperature. (a) The relationship determined by Ege and Krogh (1914) for a single goldfish. This represents the acute thermodynamic response to temperature. Data are plotted from table 1 in Ege and Krogh (1914) and show oxygen consumption rates of the same individual at different temperatures. (b) Relation between environmental temperature and resting metabolic rates for 68 species of teleost fish. This is the evolutionary relationship. Note how different species have evolved low/high resting metabolic rates depending on the environmental temperature range they are adapted. Redrawn after Clarke and Johnston (1999).

represents a frontier in the field of Earth Sciences. By bringing them together this article may help define fruitful areas of future research.

2. Temperature-dependency of metabolism

Thermal energy influences organic chemical interactions in ways that affect macromolecular structures and biochemical reactions. Higher environmental thermal energy means higher kinetic energy of biomolecules which in turn is translated into increased rates of cellular processes and increased organismal activity. The effects are not so noticeable in endothermic (warm-blooded) animals like ourselves which expend much energy to maintain a high and constant internal temperature and rapid metabolism, but they strongly affect exothermic organisms including, in the marine realm, microbes to fish (Fig. 1). This link between environmental temperature and molecular kinetics forms the basis of the temperature dependence of metabolism. Metabolism is the sum of all enzyme-driven chemical reactions within a cell (e.g., Moyes and Schulte, 2008). Most of these reactions require adenosine tri-phosphate (ATP) as fuel, so that the central process in cellular metabolism is the production of ATP (e.g., Moyes and Schulte, 2008). Metabolic rate is defined as the rate at which energy (ATP) is produced and it is measured indirectly by measuring the rate at which oxygen is consumed and CO₂ produced (respiration) (Fig. 1). For autotrophs, the metabolic rate is equal to the rate of photosynthesis because they reduce carbon dioxide to carbohydrates using energy provided by the sun (i.e., photons) to fix carbon (Brown et al., 2004).

Importantly, the temperature-dependencies of photosynthesis and respiration differ markedly, with respiration having a greater temperature sensitivity than photosynthesis (e.g., Brown et al., 2004; Allen et al., 2005; Chen et al., 2012). For autotrophs, the temperature driven antagonistic effects of oxygen and carbon dioxide binding with Rubisco during photosynthesis lead to comparatively low response rates when temperature increases (Allen et al., 2005; Lopez-Urrutia et al., 2006; Chen et al., 2012; Regaudie-de-Gioux and Duarte, 2012). For both respiration and photosynthesis the temperature-dependent increase in reaction rates continues until the optimal temperature for an organism is reached (Fig. 1), beyond this thermal threshold destructive effects begin (e.g., damages to cells and tissues in animals; Moyes and Schulte, 2008).

2.1. Temperature sensitivity of metabolism: descriptions of rate effects

It can be broadly stated that metabolism increases exponentially with temperature (Fig. 1). However, the rate of such exponential increase differs among different organisms, reactions and temperature ranges. Empirical studies describe temperature sensitivity of biological processes (from enzymatic reactions to muscle contraction) using either

the so-called Q_{10} formula or the Arrhenius equation (Cossins and Bowler, 1987; Moyes and Schulte, 2008):

1. Q_{10} formula

Q_{10} is defined as the ratio between reaction rates at two temperatures separated by 10 °C. For many physiological processes, a 10 °C increase in temperature typically doubles ($Q_{10} = 2$) or triples ($Q_{10} = 3$) the rate of the process (Moyes and Schulte, 2008).

2. Arrhenius equation:

$$k = Ae^{(-E_a/RT)} \quad (1)$$

Where k is a rate coefficient, R is the gas constant, T is temperature, A is the exponential factor, and E_a is the activation energy (e.g., Brown et al., 2004).

The use of Q_{10} originates from the first empirical temperature-rate observations and attempts to mathematically quantify the observed relation. It can also be derived independently from the theoretical equation for temperature dependence of equilibrium reactions of Van't Hoff (Berthelot, 1862; Van't Hoff, 1896; see Cossins and Bowler, 1987). The Arrhenius equation can also be traced back to Van't Hoff, and represents a further development of his work (Cossins and Bowler, 1987). According to the Arrhenius equation, the sensitivity of a reaction to temperature reflects the activation energy of the process. In chemical reactions the activation energy is the kinetic energy required for a molecule to convert to its transition state and start a chemical reaction. By increasing molecular kinetic energy, higher temperature allows more molecules to reach an energy level greater than the activation energy, increasing the likelihood of a chemical reaction (Moyes and Schulte, 2008; Kremer et al., 2017). At a given temperature only a certain proportion of molecules with energy level greater than the activation energy will react. However, following an increase in temperature the proportion of molecules with an energy greater than the activation energy increases exponentially (Cossins and Bowler, 1987). Using Q_{10} we may state that a $Q_{10} = 2$ indicates a doubling of the proportion of molecules which reach an energy level greater than the activation energy at a given temperature $T_2 = T_1 + 10$ °C.

Cellular biochemistry and biophysics allow us to understand how metabolic temperature-dependency works at the cellular level i.e. how a certain increase in temperature is translated into an increase in cellular metabolism. Temperature increases the kinetic energy of cellular molecules and enzymes, so that cellular processes are driven faster because of a larger number of molecules possessing enough energy to overcome the energy barrier imposed by the activation energy. This in turn stimulates the production of ATP because more ATP is required to fuel higher rates of cellular reactions. This is the acute thermodynamic effect of temperature on the organism until acclimation takes effect (Fig. 1a) (Clarke, 2004; Clarke and Fraser, 2004). To the opposite, the

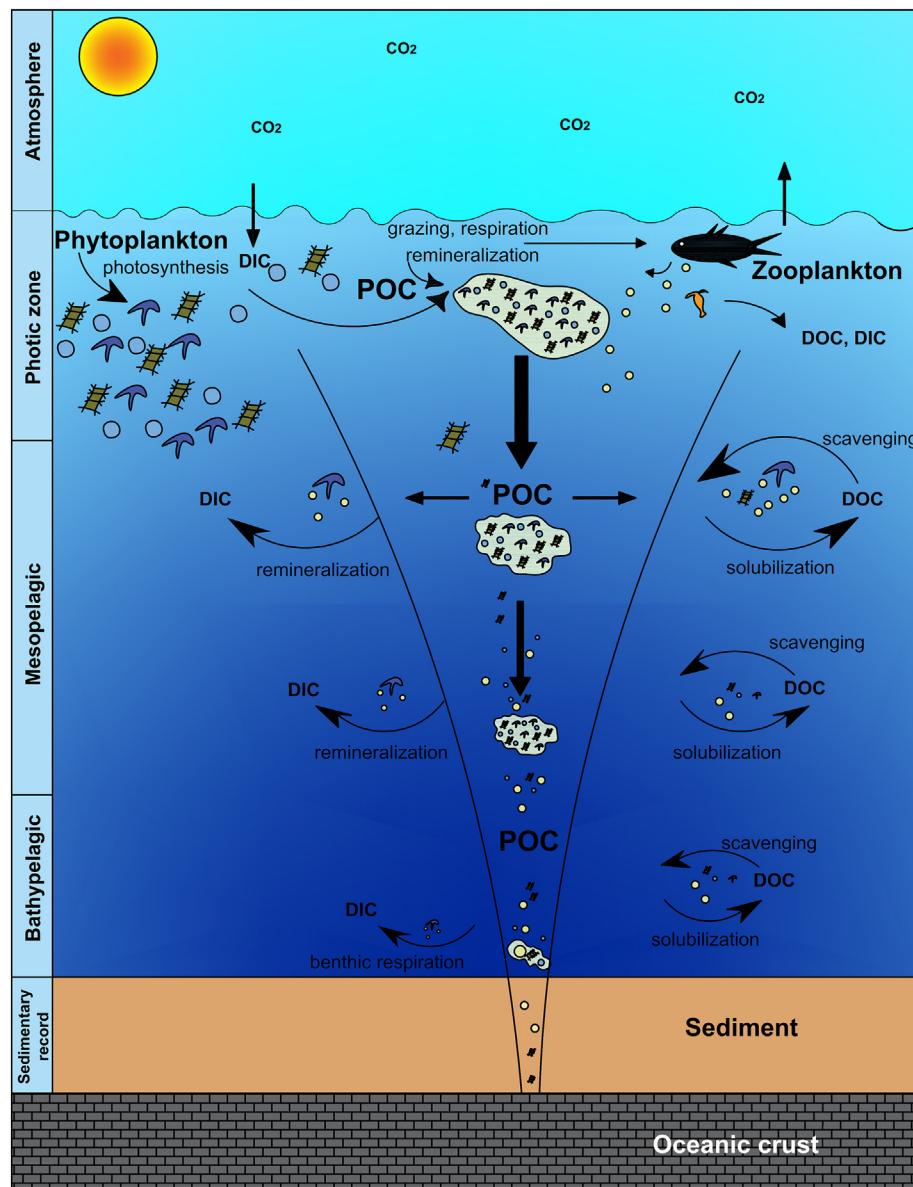


Fig. 2. Schematic of the components of the biological pump. Photic zone: 0–100 m; Mesopelagic: 100–1000 m; Bathypelagic: 1000 to abyssal depths. Below 1000 m depth carbon is considered removed from the atmosphere for at least 100 years (see main text). Scavenging: DOC incorporation within sinking particles.

average metabolic rate of any species at its normal environmental temperature represents the result of the evolution for that species, influenced by temperature, ecology and life history (Fig. 1b) (Clarke, 2004; Clarke and Fraser, 2004). The acute thermodynamic response to temperature is also considered to be set by a species evolution within a certain range of environmental temperatures which in turn determines that species temperature sensitivity (e.g., Clarke and Fraser, 2004).

2.2. Theoretical ecology: the Universal Temperature Dependency and the Metabolic Theory of Ecology

From around the time that Van't Hoff (1896) and Arrhenius (1889, 1915) described the theoretical dependence of inorganic chemical reaction rates on temperature, multiple laboratory studies empirically showed the same for biological processes (e.g., Vernon, 1894, 1897; Ege and Krogh, 1914; Krogh, 1916; Shapley, 1920; Spoor, 1946; Eppley, 1972; Sibly et al., 2012 for a review). In 2001, Gillooly and coauthors integrated the evidence from empirical biological studies with the theoretical foundations of temperature-dependency in inorganic

reactions – the Arrhenius equations along with the Maxwell-Boltzmann frequency distribution law – to generate a new ecological theory which they called Universal Temperature Dependency (UTD) (Gillooly et al., 2001). UTD was conceived to create a common framework for physiology and ecology based on theoretical biochemistry and biophysics. It relies on an equation designed by Gillooly et al. (2001) to couple the Arrhenius equation to the body size scaling coefficient of organismal metabolism (e.g., Kleiber, 1932; Hemmingsen, 1950):

$$Q = b_0 M^{3/4} e^{(-E/kT)} \quad (2)$$

where Q is the metabolic rate of any organism, M is body mass, T is absolute temperature, k is Boltzmann's constant, E is the activation energy of metabolism (defined as the average activation energy for the rate-limiting enzyme-catalyzed biochemical reactions of metabolism) and b_0 is a scaling constant independent of M and T (Gillooly et al., 2001). This equation states that organism metabolism, and hence all biological processes depending on the organismal production of energy, scale according to body size and temperature. With this equation the same thermodynamic laws governing temperature dependency of

inorganic reaction rates apply to the pathway of reactions which compose organismal metabolism. In effect, Gillooly and coauthors described temperature-dependency of metabolism as a universal phenomenon driven by thermodynamics and underpinning the whole physiology of animals and plants (Gillooly et al., 2001). A similar temperature-dependency is assumed for all respiration-like processes, and this poses the basis for a broader ecological theory, the Metabolic Theory of Ecology (MTE), (Brown et al., 2004). Building upon UTD, the MTE states that most of the variation in rate processes can be explained by differences in body size and temperature, as mediated by metabolic rate. With this theory, metabolism becomes a dominant active driver within the Earth system, a “pacemaker” capable of altering the flux of elements between organisms and the environment, and shaping communities and ecosystems. MTE has been defined as a mechanistic, quantitative, synthetic framework that (1) characterizes the effects of body size and temperature on the metabolism of individual organisms; and (2) characterizes the effect of individual organisms on the pools and flows of energy and matter in populations, communities and ecosystems (Brown et al., 2004). This is based on MTE explicit predictions for the value of activation energies, depending on which biochemical process is rate-limiting. For instance for heterotroph respiration this is ATP synthesis with an activation energy of 0.65 eV (Kremer et al., 2017). Hence, within the framework created by MTE, metabolism-scaling allows the description of large ecosystem-scale changes.

UTD and MTE rely on a number of assumptions (e.g., Dell et al., 2011; Huey and Kingsolver, 2011; Glazier et al., 2015) and as such have attracted considerable criticism (Clarke and Fraser, 2004; Clarke, 2004). Nonetheless, these theories have stimulated a wave of interest, with a growing body of studies providing refinements, empirical support and raising new challenges (e.g., Price et al., 2012; Rall et al., 2012; Lemaître et al., 2014; Bruno et al., 2015; Alcaraz, 2016; Pawar et al., 2015; Kremer et al., 2017). More importantly, MTE provides the context for understanding the Earth and its history as a system including a shared horizon for fields of research that were traditionally very distant.

3. A temperature-dependent biological pump?

The ocean sequesters a third to a quarter of the carbon released by human activities each year (Sabine et al., 2004; Khatiwala et al., 2009) and the transfer of this carbon to the interior of the ocean depends partly on the functioning of the biological pump (Fig. 2) (Passow and Carlson, 2012). The ocean is also absorbing much of the excess heat produced by human activities and is warming rapidly (Levitus et al., 2000; Pörtner et al., 2014). Therefore, it is important to consider how the biological pump will respond to increasing ocean temperature in the near and further climate future.

Could metabolic temperature-dependency impact the functioning of the biological pump? Between the late eighties and the nineties, the Joint Global Ocean Flux Study (JGOFS) oceanographic program to study the ocean carbon cycle, provided the first field-based evidences of links between temperature and ocean carbon biogeochemistry (Laws et al., 2000). This evidence fed into the linked Synthesis and Modelling Program (SMP), which provided the first theoretical and numerical model descriptions of the relationship between temperature and changes in export production. (e.g., see Laws et al., 2000). According to MTE, the temperature- and size-dependent scaling of biological processes allows us to predict and describe the responses to increasing temperature at ecosystem and higher levels. Empirical studies show a particularly strong temperature-dependency for marine biological rates (Fig. 1) (e.g., Ege and Krogh, 1914; Eppley, 1972; Clarke and Fraser, 2004; O'Connor et al., 2009; Lassen et al., 2010; Taucher et al., 2012; Yvon-Durocher et al., 2015a; Kremer et al., 2017). Marine organisms are mostly ectotherms, and water has a greater thermal conductivity than air (Cossins and Bowler, 1987). This suggests that the biological pump may be sensitive to increasing ocean temperature via

temperature-induced increases in respiration and photosynthesis rates, and changes in nutrient biogeochemical cycling. In the following section we describe the flux of carbon to the deep ocean via the biological pump, and summarize different mechanisms through which metabolic temperature dependency may impact the functioning of the biological pump and eventually the carbon cycle, representing a potential biological feedback for global climate.

3.1. The biological pump and carbon sequestration flux

In order to understand how metabolic temperature-dependency might affect the biologically mediated transport of carbon to the inner ocean (biological pump), it is important to identify what controls such transport (Fig. 2). The biological pump has two components, the organic carbon pump and the calcium carbonate pump (Passow and Carlson, 2012). The organic carbon pump is defined as a combination of biologically driven processes which spatially separate organic matter production from remineralization (Fig. 2) (Passow and Carlson, 2012; Meyer et al., 2016). The other component, the calcium carbonate pump, consists of the biological incorporation and transport of carbon in calcium carbonate shells (Passow and Carlson, 2012). The organic carbon pump has a greater efficiency in exporting carbon than the calcium carbonate pump (Hülse et al., 2017), and on short time scales the calcium carbonate pump is counteracted by the production of CO₂ during CaCO₃ secretion by marine calcifiers (e.g., Ridgwell and Zeebe, 2005). In this review we mainly focus on the organic carbon pump and from now on the term biological pump refers the organic carbon component.

Carbon (from dissolved CO₂), is fixed into Particulate Organic Carbon (POC) via photosynthesis in the euphotic zone (upper ~100 m of the water column). Depending on location, between about 1 to 40% of photosynthetically fixed carbon is exported into the dark realm of the ocean where it is remineralized at much slower rates than in surface waters (Fig. 2) (Herndl and Reinthaler, 2013). The remineralization depth is the average depth at which sinking particulate organic carbon is converted back to carbon dioxide and it is set by the balance between particle sinking speeds and their rate of decay (Kwon et al., 2009; Weber et al., 2016). This in turn is controlled by multiple factors such as POC density and ballasting with minerals or organic polymers, and water column temperature (Laws et al., 2000; Wilson et al., 2012; Iversen and Ploug, 2013). Heterotrophic bacteria living attached to sinking particulate organic matter are responsible for organic matter remineralization at mesopelagic (100–1000 m) and bathypelagic (1000–4000 m) depths and account for roughly half all respiration in the ocean, the other half occurring in the euphotic zone (Fig. 2) (Sarmiento et al., 2010). In eutrophic regions – dominated by micro-phytoplankton such diatoms – zooplankton degradation contributes significantly to the rapid reduction in particle flux in mesopelagic waters (Herndl and Reinthaler, 2013; Steinberg and Landry, 2017). According to Giering and co-workers, the activity of zooplankton fuels microbial respiration by producing slow sinking particulate matter and dissolved organic matter that is subsequently remineralized by microbes, with prokaryotes responsible for 70 to 90% of remineralization below the photic zone (Fig. 2) (Giering et al., 2014).

By convention, carbon fixed into organic matter is considered sequestered when it is transported below 1000 m water depth (Passow and Carlson, 2012). The flux to below 1000 m depth is called the sequestration flux because the carbon which reaches this depth is removed from the atmosphere for at least 100 years (Fig. 2) (Passow and Carlson, 2012). Hence, the global magnitude of the sequestration flux helps set the carbon storage within the inner ocean and the effectiveness of the biological pump in removing carbon from the upper ocean / atmosphere system. In turn the sequestration flux is controlled by the following upper ocean physical and biological properties and processes (e.g., Passow and Carlson, 2012; Herndl and Reinthaler, 2013):

- Composition of the phytoplankton community in the surface ocean,

nutrient availability and light affect rates of carbon fixation;

- Intensity of flux attenuation between the base of the euphotic zone and through the mesopelagic zone (100 to 1000 m);
- Adherence to Redfield stoichiometry of phytoplankton biomass and exported organic matter;

Each of these factors has a major role in determining the magnitude of the sequestration flux and hence the efficiency of the biological pump. In this review we refer to the efficiency of the biological pump as the ratio of carbon exported from the surface layer of the ocean to the total amount of carbon produced by phytoplankton primary production (Herndl and Reinthaler, 2013).

Therefore, it is of key importance to address how the above factors may in turn be affected by metabolic temperature-dependency in a warming (or cooling) ocean.

3.1.1. Composition of phytoplankton community

Particulate organic carbon sinks mostly in the form of marine snow (clumps of aggregated phytoplankton, discarded appendicularian houses, fecal matter, and other miscellaneous detrital particles), large phytodetrital aggregates and fecal pellets (Turner, 2015). Diatoms are the predominant producers of phytoplankton aggregates because they are capable of voluminous production of transparent exopolymer particles which glue organic particles together (De La Rocha and Passow, 2007; Turner, 2015; Tréguer, 2018). Aggregates are bigger than marine snow and fecal pellets and tend to have greater sinking velocities so that where diatoms are the main phytoplankton group there tends to be a very efficient export of organic matter out of the euphotic zone (De La Rocha and Passow, 2007; Herndl and Reinthaler, 2013; Le Moigne et al., 2015; Agusti et al., 2015; Turner, 2015). At the opposite extreme, in oligotrophic regions, picophytoplankton – mostly cyanobacteria in the size range 0.2–2 μm – produce organic carbon which is thought to undergo faster remineralization in the euphotic zone due to their very small size (De La Rocha and Passow, 2007; Moran et al., 2010; Herndl and Reinthaler, 2013). Hence, irrespective of temperature-dependency, there appears to be a coupling between phytoplankton community structure in the euphotic zone, the size of the particles exported, and the particle flux through the mesopelagic layer (Laws et al., 2000; Guidi et al., 2009, 2015; Herndl and Reinthaler, 2013; Siegel et al., 2016).

Moran et al. (2010) compiled large time-series of picophytoplankton abundances in the temperate North Atlantic and found remarkable correlations between abundance, cell size and temperature. Crossing a temperature increase of 30 $^{\circ}\text{C}$ (from -5° to 25°C) they found that the relative abundance and biomass of picophytoplankton increased, whereas picophytoplankton cell size and total phytoplankton biomass decreased (Moran et al., 2010). According to the authors, a combination of temperature and nutrient availability (nutrient concentration generally decreases toward warmer regions) can explain the observed patterns. Therefore in a warming ocean picophytoplankton may become more dominant if the adjustment of phytoplankton composition is consistent over time as it is over space (Moran et al., 2010). Given its lower transfer efficiency (i.e., low export from the euphotic zone to 1000 m; Weber et al., 2016) a relative increase in picophytoplankton-produced organic carbon could progressively lead to a less efficient biological pump, as a greater fraction of primary production would be channeled through the upper ocean microbial loop (Fig. 3) (Jiao et al., 2010; Regaudie-De-Gioux and Duarte, 2012).

This possibility received support from Weber et al. (2016) who reconstructed global deep ocean particle fluxes by diagnosing the rate of nutrient accumulation along transport pathways in a data-constrained ocean circulation model. In that study, among all the variables considered, the size and structure of the phytoplankton community was the best predictor of particle transfer efficiency. The fraction of biomass contributed by picophytoplankton, which varies between $> 55\%$ in the subtropics and $< 30\%$ in subarctic regions, explained up to 93% of the variance in transfer efficiency between regions (Weber et al., 2016).

Yet, other studies show that small cells (i.e., picophytoplankton ($\leq 2 \mu\text{m}$) and nanophytoplankton ($> 2 \mu\text{m}$ to $20 \mu\text{m}$) can contribute to the downward carbon flux e.g., through food-web interactions resulting in faster production of fecal pellets. These studies suggest that in areas where nano and picophytoplankton are dominant, the transfer efficiency can actually be higher than in areas dominated by microphytoplankton (Richardson and Jackson, 2007; Guidi et al., 2009, 2015; Herndl and Reinthaler, 2013; Puigcorb  et al., 2015; Bach et al., 2016), even though the amount of organic carbon which reaches the sea-floor is lower overall than in productive regions (Fig. 3) (Guidi et al., 2009; Herndl and Reinthaler, 2013).

A recent survey conducted in the North Atlantic challenges the idea that particle size – and hence phytoplankton community composition – has a dominant role in determining transfer efficiency (Marsay et al., 2015). In the North Atlantic the transfer efficiency appears to be mostly a function of temperature in the mesopelagic zone setting the rate of organic matter remineralization (flux attenuation, see paragraph 2.1.2), with similar sinking velocities for aggregates produced in cold and warm North Atlantic regions (Marsay et al., 2015). While this result appears inconsistent with other POC flux studies that found lower transfer efficiency in high latitude colder waters (e.g., Francois et al., 2002; Henson et al., 2012), Marsay et al. (2015) proposed that POC “quality” (i.e., the existence of more highly labile POC in cold waters) could explain the inconsistencies between their study and others.

Despite these debates, this field of research is rapidly developing and it seems safe to assume that both temperature and community composition significantly affect the efficiency of the biological pump. Further studies analyzing biological and physical ocean properties (phytoplankton community composition, water column temperature profiles, particle flux, and flux attenuation; see for instance Siegel et al., 2016) across latitudinal and nutrient gradients will help to improve our understanding on how changes in phytoplankton community composition with global warming may ultimately affect carbon export.

3.1.2. Intensity of flux attenuation

The reduction in organic matter flux between the base of the photic and the mesopelagic zone is referred to as flux attenuation and is caused by intense biological remineralization and solubilization during downward transport (Figs. 2, 4) (Laws et al., 2000; Passow and Carlson, 2012). Remineralization is the process of converting organic carbon to inorganic carbon through eating and decomposition; solubilization refers to the conversion of particulate organic carbon to Dissolved Organic Carbon (DOC) (Passow and Carlson, 2012). These biological processes reduce the downward export of organic matter (and carbon) by on average 90% in the upper 1000 m (Passow and Carlson, 2012), and allow carbon to be recycled in the water column instead of being sequestered at greater depths (Figs. 2, 4). There are at least two main ways by which temperature-dependency of metabolism might affect the intensity of flux attenuation:

(1) Increasing heterotroph grazing pressure on phytoplankton communities;

This may result primarily from the different temperature-dependency of photosynthesis and respiration set by their different activation energies, with respiration activation energy ($\sim 0.6\text{--}0.7 \text{ eV}$) determined by the production of ATP from glycolysis and the tricarboxylic acid cycle, and that of photosynthesis set by Rubisco carboxylation ($\sim 0.32 \text{ eV}$) (Allen et al., 2005; Chen et al., 2012). The MTE predicts that the different activation energies for respiration and photosynthesis are constant among heterotrophic and autotrophic taxa, and scale up to community levels (Brown et al., 2004; Allen et al., 2005; Lopez-Urrutia et al., 2006). This is increasingly being tested using culture experiments (e.g., O'Connor et al., 2009; Chen et al., 2012) and global data sets for community respiration and photosynthesis (Laws et al., 2000; Regaudie-De-Gioux and Duarte, 2012; Yvon-Durocher et al., 2012), with results that closely match those from theoretical models. This implies that in a warming ocean, respiration rates (i.e., heterotroph

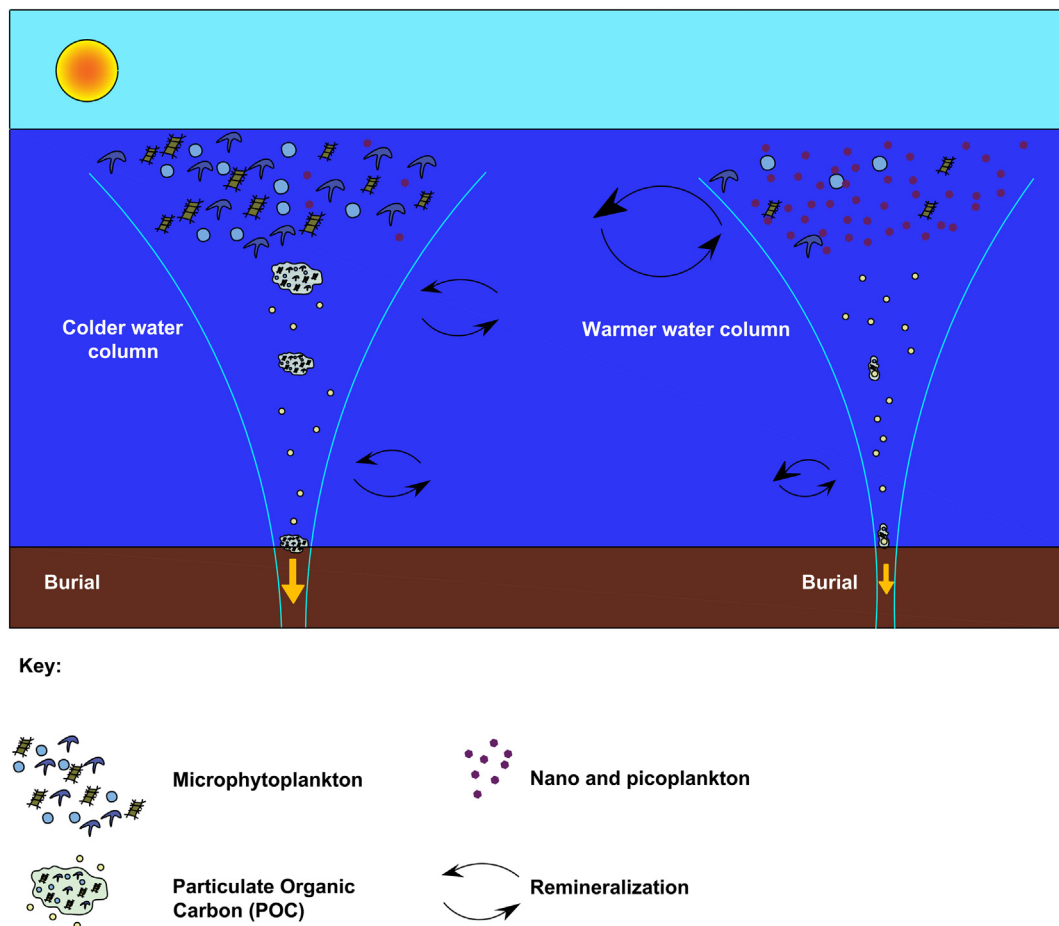


Fig. 3. A temperature-dependent biological pump. Illustrative cartoon showing the effects of different water temperatures on organic carbon export and remineralization: more carbon is sequestered when temperature is colder compared to when is warmer.

metabolism) would increase more than the rate of photosynthesis and gross primary production, with a consequent increase in grazing pressure of herbivore microzooplankton on phytoplankton. Regaudie-De-Gioux and Duarte (2012) showed that communities in water warmer than 21 °C tend to be heterotrophic (i.e., dominated by consumers as opposed to primary producers), and calculated a decline of the productivity-respiration ratio (P/R) of planktonic communities with increasing temperature. From this relationship, the authors predicted a 25% decrease in P/R for the 4 °C ocean warming possible by the end of the current century (IPCC, 2013), suggesting that large ocean areas may switch from carbon sinks into carbon sources. Similarly, in an indoor mesocosm study, Paul et al. (2015) evaluated the effect of temperature increase on Baltic Sea plankton communities, and found a stimulation of phytoplankton blooms which at the same time are subject to a stronger top-down control by zooplankton. O'Connor et al. (2009) and Chen et al. (2012) studied microzooplankton communities and found that grazing pressure increases with temperature in meso-eutrophic environments, leading to a decrease in phytoplankton biomass due to excess grazing (Chen et al., 2012) and eventually to a decrease in microzooplankton standing stocks due to resource exhaustion (O'Connor et al., 2009). Olonscheck et al. (2013) tried to deconvolute the physical and biological effects of warming on chlorophyll *a* concentrations under a scenario of unabated anthropogenic carbon emissions. Using a coupled ocean general circulation and carbon cycle model they found that much of the observed decline in chlorophyll *a* concentrations can be attributed to the different temperature sensitivities of phyto- and zooplankton, rather than to physically driven processes such as increased ocean stratification.

Increased grazing pressure would primarily lead to less CO₂ fixed by

photosynthesis thus weakening the role of the biological pump at the initial stage of organic carbon cycling in the ocean. Secondly, more organic carbon would be channeled through pelagic food webs and hence recycled, and less would be left to form marine snow aggregates sinking to greater depths (Fig. 3) (e.g., Laws et al., 2000; Turner, 2015).

(2) Increasing rates of organic matter remineralization, decreasing oxygen and pH;

Sarmiento et al. (2010) compiled a study with both empirical observations and theoretical predictions to describe the behavior of euphotic zone-dwelling bacteria to ocean warming. They argued that higher temperatures will increase bacterial respiration of organic carbon and enhance remineralization of particulate organic matter. In a laboratory experiment, Iversen and Ploug (2013) measured the influence of surface water and thermocline temperatures (15° and 4 °C) on diatom aggregate sinking speed and bacteria carbon-specific respiration rates. They found lower community respiration rates in the aggregates at 4 °C compared to those measured at 15 °C due to lower cell specific activities within aggregates, and concluded that ambient temperatures significantly affects organic matter remineralization by microbiota. In line with these experimental observations and theoretical predictions, Marsay et al. (2015) revealed decreasing mesopelagic particulate organic carbon fluxes moving horizontally from cold to warm regions of the North Atlantic, and attributed this pattern to increased efficiency of mesopelagic organic matter remineralization in regions where ocean temperature is higher. A similar pattern has also been recently reproduced using a particle flux model (Cram et al., 2018). Not only horizontal, but also vertical changes in the rate of organic matter decay in the ocean are temperature-dependent, with remineralization rates following temperature-depth profiles (Marsay et al., 2015; Brewer and

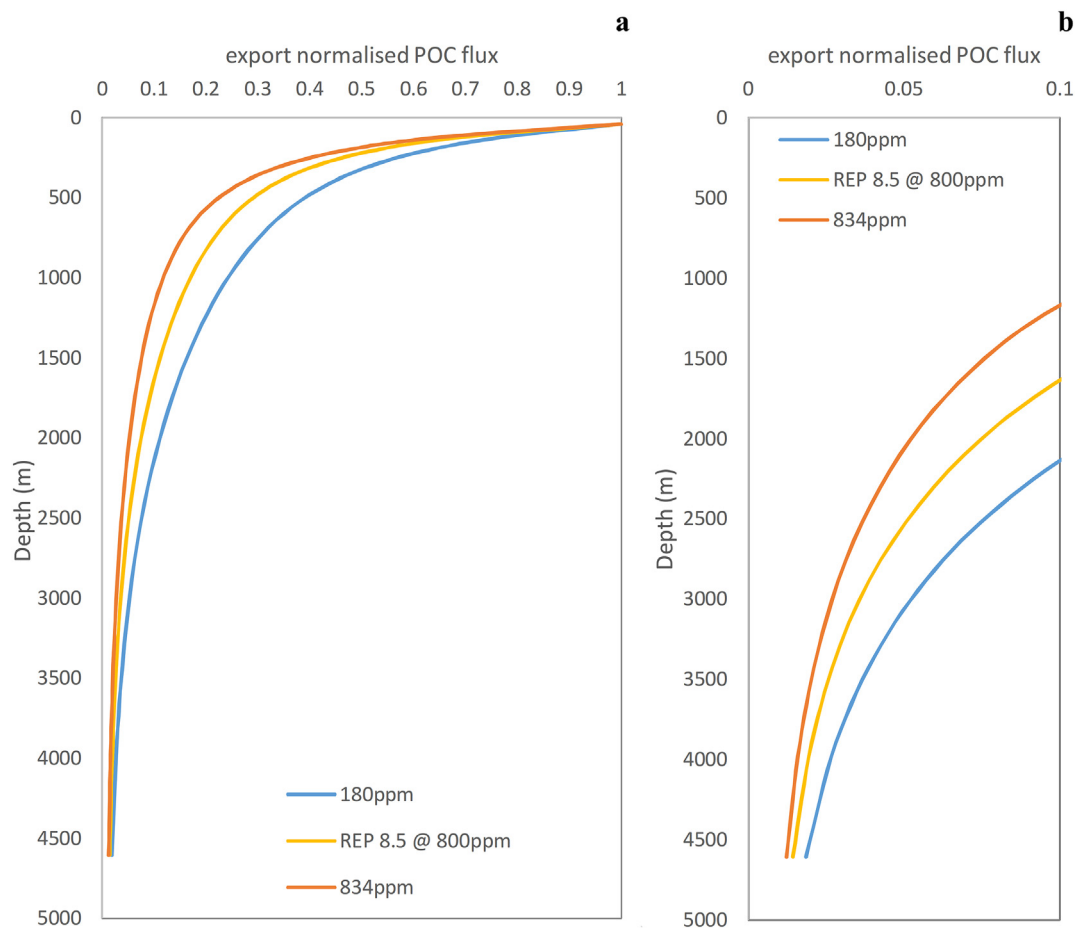


Fig. 4. a: Full range of modelled global mean POC flux normalized to export production. Blue line: 180 ppm atmospheric CO_2 ; Orange line: 834 ppm atmospheric CO_2 ; Yellow line: Representative Emissions Pathway (REP) 8.5 at 800 ppm atmospheric CO_2 . The blue line represents a scenario where the ocean is globally cooler. The orange line represents a scenario where the ocean is globally warmer, the yellow line represents a potential future scenario of atmosphere-driven warming where only the surface ocean warms up. b: Close up of the lower range of values of modelled global mean POC flux normalized to export production. Model simulations: model set-up with temperature-dependent remineralization as in [John et al., \(2014\)](#) and present-day continental configuration. 180 ppm: cGenie at end of spin-up (10 k years) at 180 ppm; 834 ppm: cGenie at end of spin-up for (10 k years) at 834 ppm; Representative Emissions Pathway (REP) 8.5 at 800 ppm: cGenie spin-up for 10 k years at 280 ppm, thereafter forced with atmospheric CO_2 from REP 8.5 driven CLIMBER-2 model output ([Crichton et al., 2016](#)). Time slices taken at year 2080C.E.

[Peltzer, 2016, 2017; Weber et al., 2016; Meyer et al., 2016; Laufkötter et al., 2017](#)). This is also shown in [Fig. 4](#) where we report decreasing POC flux estimates obtained from cGenie model simulations by parameterizing temperature-dependent organic matter remineralization rates under increasingly high atmospheric pCO_2 . In a warming ocean, microbial remineralization of particulate organic matter would increase, leading to a greater attenuation of particle flux at mesopelagic depths, i.e., a shallower average remineralization depth ([Figs. 3, 4](#)). Shallow remineralization depths occur in warm waters where respiration processes are fast and most of the organic matter is respired back in the euphotic zone. In cold waters respiration is slower and more POC reaches mesopelagic depths, so that the remineralization depth is on average deeper ([Kwon et al., 2009; Laufkötter et al., 2017](#)). The remineralization depth sets the depth at which respired nutrients are transferred to the deep ocean ([Weber et al., 2016](#)). Hence, on a global scale, a deepening/shallowing of the remineralization depth can substantially affect the redistribution of dissolved carbon between the upper and inner ocean, and hence the strength of the sequestration flux ([Kwon et al., 2009; Menviel et al., 2012; Segschneider and Bendtsen, 2013; Roth et al., 2014](#)).

Increasing ocean temperature combined with higher rates of organic matter respiration would have the secondary effects of decreasing oxygen levels – potentially expanding oxygen minimum zones – and

decreasing pH at depth (e.g., [Laws et al., 2000; Pörtner et al., 2014; John et al., 2014; Brewer and Peltzer, 2016; Meyer et al., 2016; Laufkötter et al., 2017](#)). This is likely to affect micro and mesozooplankton by reducing zooplankton diversity and population density, compressing toward the surface the vertical habitat of zooplankters living at mesopelagic depths, and eventually causing habitat reductions ([Stramma et al., 2012; Sperling et al., 2013, 2016; Deutsch et al., 2014](#)). The role of zooplankton in the cycling of carbon below the euphotic zone is multifaceted and complex ([Turner, 2015; Steinberg and Landry, 2017](#)), however it is likely to shrink with ocean warming as larger multicellular organisms such as copepods are more sensitive to decreases in oxygen and pH than microbial respirers ([Pörtner et al., 2014; McCormick and Levin, 2017](#)). This may be associated with an expansion and increased efficiency of the microbial carbon pump with greater amounts of POC transferred to the pool of Recalcitrant Dissolved Organic Carbon (RDOC; [Jiao et al., 2010, 2014](#)), in parallel with a reduction of the sequestration flux and hence of the efficiency of the biological pump ([Fig. 3](#)) ([Matsumoto et al., 2007; Roth et al., 2014](#)). While the slow cycling of RDOC prolongs the residence time of carbon in the ocean ([Jiao et al., 2010](#)), large amounts of POC converted to RDOC would ultimately reduce the sedimentary burial of organic carbon and its sequestration over geologic time intervals ([Olivarez-Lyle and Lyle, 2006](#)).

3.1.3. Redfield stoichiometry of phytoplankton biomass and exported organic matter

The cellular contents of carbon (C), nitrogen (N), phosphorus (P), and other elements in marine phytoplankton are emerging as important features of ocean biogeochemistry. For a long time, C/N/P was assumed static at Redfield proportions (106/16/1; Redfield, 1958). However, recent work has demonstrated significant differences in the elemental content and ratios of marine phytoplankton communities across regions or seasons (e.g., Martiny et al., 2016 and reference therein). The exact mechanisms controlling the observed regional differences are still uncertain as key environmental factors strongly co-vary in the ocean. Nevertheless, temperature has been proposed as a relevant factor for setting the elemental allocation in marine phytoplankton (Martiny et al., 2013; Toseland et al., 2013; Yvon-Durocher et al., 2015b). Toseland and co-workers (2013) showed that phytoplankton produce more P-rich ribosomes at lower temperatures possibly to compensate for lower translational efficiency, i.e. lower rates of protein synthesis. At higher temperatures eukaryotic phytoplankton seem to require a lower density of ribosome because the synthesis of N-rich proteins increases strongly.

These data suggest that temperature influences cellular resource allocation via its effects on cellular core-metabolism, eventually changing the elemental ratios in phytoplankton, such that warming of the oceans would lead to increasing N/P ratios of marine communities (Toseland et al., 2013). This is supported by recent work demonstrating a positive correlation between the N/P ratio of algal biomass and latitudinal variation in sea-surface temperature (Martiny et al., 2013; Yvon-Durocher et al., 2015b), and by a meta-analysis of eukaryotic phytoplankton lineages, which detected an increase in C/P and N/P for cells growing at higher temperature (Yvon-Durocher et al., 2015b).

Changes in the N/P stoichiometry of marine plankton, and specifically increase in N/P will tend to increase N limitation in the ocean, but may also increase export fluxes of carbon given that C/N is relatively conserved (Toseland et al., 2013). A recent model study suggests that by altering the C/P of exported organic matter, latitudinal changes in plankton stoichiometry may be transferred to the pool of deep ocean nutrients despite the homogenizing action of ocean overturning circulation (Teng et al., 2014). Increased marine plankton C/N/P, may hence represent a negative feedback to the weakening of the biologic pump's efficiency. This negative feedback might in turn be counteracted by increased nitrogen limitation in the ocean and thus decreased primary productivity (further enhanced by increased stratification due to warming) or by shifted phytoplankton composition toward phytoplankton groups that reduce POC transfer efficiency. Variable stoichiometry within phytoplankton may also have cascade effects on the cycling of major ocean nutrients by altering the relative contribution of the microbial carbon pump in the ocean (Jiao et al., 2010), with more dissolved organic matter converted to recalcitrant forms (i.e., a more efficient microbial carbon pump) when phytoplankton stoichiometry is unbalanced (C-rich; Polimene et al., 2017).

4. The long term carbon cycle

From the considerations discussed above, it follows that a temperature-dependent biological pump may indeed affect carbon export and eventually lead to a lower carbon sequestration flux, i.e. to less carbon being exported below 1000 m water depth, and hence sequestered from the atmosphere for at least 100 years (Fig. 4). The effects of such a reduction of bathypelagic fluxes of carbon may be far reaching. Any mechanism that alters the distribution of carbon between the upper and deep ocean ultimately changes the steady-state cycling of carbon. Less carbon exported below 1000 m depth could lead to less carbon reaching the sea-floor and being buried within sediments (Fig. 4). While pelagic burial of organic carbon is a small component of the carbon cycle (0.01 Gt C/yr), it constitutes a significant carbon sink over relatively short geological time spans if uncompensated (Olivarez-Lyle and

Lyle, 2006). Further, ocean-sediment interactions can amplify or mitigate a perturbation in the ocean-atmosphere system (Roth et al., 2014). For instance, more carbon buried means more carbon removed from the global system and sequestered within the rock reservoir, hence a higher capacity of the ocean to absorb atmospheric CO₂ (Broecker, 1982). Model studies show that lower rates of POC degradation associated with a deepening of the remineralization depth of the order of just tens of meters can account for ~10–30 ppm changes in atmospheric CO₂ concentrations (Matsumoto et al., 2007; Kwon et al., 2009; Chikamoto et al., 2012; Menviel et al., 2012; Segsneider and Bendtsen, 2013; Roth et al., 2014). This stems not only from changes in the atmosphere-ocean partition of carbon, but also via impacts on the long-term carbon cycle by disturbing the weathering-burial balance of carbon, alkalinity and nutrients. The downward shift of respired carbon causes dissolution of sediment CaCO₃ and hence increased ocean alkalinity (Boyle, 1988), while further longer-term sediment feedbacks associated with both POC and CaCO₃ burial alter surface water nutrient concentrations (Kwon et al., 2009; Roth et al., 2014). These changes in water chemistry lead to more CO₂ absorbed by the ocean when more dissolved inorganic carbon (DIC) is stored and buried in the deep ocean and vice versa (Fig. 4) (Matsumoto et al., 2007; Kwon et al., 2009; Segsneider and Bendtsen, 2013; Roth et al., 2014).

5. Metabolic temperature dependency and past climate

Weathering of silicates in the continental crust has long been considered the dominant long-term thermostat for Earth's climate (Bernier and Caldeira, 1997). However, in 2006 Olivarez-Lyle and Lyle suggested a link between temperature-dependency of metabolic rates in the ocean, and the long-term evolution of climate (Olivarez-Lyle and Lyle, 2006). Temperature-dependency was considered as a possible feedback supporting the Eocene high-temperature and high-CO₂ climate through its effect on bacterial respiration rates and the remineralization or burial of carbon. The authors calculated mass accumulation rates of organic carbon in Eocene sediments from the palaeo-equatorial eastern-Pacific (a high productivity area because of upwelling) and found much lower organic carbon accumulation rates than expected (10–20 times lower than in Pleistocene and Holocene samples from the same area). The authors suggested that the “missing” burial of organic carbon was due to high rates of organic matter remineralization in the much warmer Eocene water column. They proposed that faster microbial respiration rates than today could have helped maintain a high dissolved inorganic carbon pool in the oceans relative to alkalinity, setting the high atmospheric CO₂ conditions of the Eocene, which lasted unabated for millions of years. With this idea, Olivarez-Lyle and Lyle (2006) offered a new perspective for interpreting ancient sedimentary records. Since then, an increasing number of studies have provided refinements, support and new challenges to the idea that metabolic temperature-dependency can feed back on the global climate state. Below we provide an overview for the Last Glacial Maximum and Eocene greenhouse climate.

5.1. The Last Glacial Maximum

With its large ice sheets, the Pleistocene (~2.6 Ma), is the coldest period in the last 66 Ma. The presence of large ice sheets had a strong control on climate and on the sequestration of carbon in the ocean (Clark et al., 1999). At the Last Glacial Maximum (LGM), (~22 ka), global temperatures were 3 to 4 °C cooler than the pre-industrial period, ice sheets much larger than today were present in both hemispheres and atmospheric CO₂ was around 190 ppm, some 100 ppm lower than during the pre-industrial period. The cause of CO₂ drawdown and cooling has been attributed to a combination of several ocean feedbacks working in the Earth system by affecting the cycling of carbon and/or the pattern of ocean and atmosphere circulation (Sigman and Boyle, 2000; Sigman et al., 2010; Hain et al., 2014). Proposed mechanisms

include: the increased solubility of carbon in cooler waters (Buchanan et al., 2016); changes in ocean circulation (Watson and Naveira Garabato, 2006; Brovkin et al., 2007; Buchanan et al., 2016; Banderas et al., 2012), possibly linked to increased sea ice extent in the Southern Ocean (Shin et al., 2003; Jansen, 2017); increased sea ice extent directly resulting in the accumulation of carbon in the deep Southern Ocean (Bouttes et al., 2011; Jansen, 2017); changes in air-sea gas exchange rates e.g., due to wind forcing (Toggweiler et al., 2006; Banderas et al., 2012; Menviel et al., 2018); and changes in ocean productivity affecting the ocean biological pump (Sigman and Boyle, 2001; Brovkin et al., 2007; Sigman et al., 2010; Schmittner and Somes, 2016). Temperature-dependent organic matter remineralization has also been considered for its potential role in Pleistocene glacial-interglacial cycles, and modelling studies have been performed to test the idea that metabolic temperature-dependency may have contributed to lower atmospheric CO₂ values during the Last Glacial Maximum (Matsumoto et al., 2007; Chikamoto et al., 2012; Menviel et al., 2012; Roth et al., 2014). These models suggest a significant role for temperature-dependent respiration in contributing to large atmospheric CO₂ changes by altering microbial POC remineralization rates and the average POC remineralization depth. Kwon et al. (2009) suggest that a downward shift of respired nutrients and carbon from the upper to the deep ocean may have contributed to further draw down atmospheric CO₂ during glacial intervals. Roth et al. (2014), show a high sensitivity of atmospheric CO₂ to changes in the POC remineralization depth which also impacted the long-term carbon cycle by disturbing the weathering–burial balance which amplifies the ocean–atmosphere response by a factor of 3–7 on multi-millennial timescales.

In warmer periods in Earth history, and in a future warmer world, non-existent or reduced ice sheets would have less impact over ocean carbon sequestration, and mechanisms affecting the biological pump and its efficiency may exert a stronger control on global climate.

5.2. Eocene greenhouse world and carbon cycle perturbations

The Eocene (~55–34Ma) was a time of much higher than today Earth surface temperatures, especially so at mid to high latitudes (Pross et al., 2012; Evans et al., 2018). Poles lacked permanent ice-caps for most of the Eocene (Pagani et al., 2014), and deep water temperatures ranged between 5 and 12.5 °C, compared to modern values globally close to 0 °C (Cramer et al., 2011). Atmospheric CO₂ levels much higher than today (600 to 1500 ppm; Anagnostou et al., 2016) were probably responsible for this dramatically different mean climate state. Temperature started to gradually cool only after the Early Eocene Climatic Optimum (EECO, ~53–50 Ma; Lauretano et al., 2015; Dallanave et al., 2016), leading to the inception of the Antarctic glaciation by the Eocene-Oligocene transition (EOT, ~34 Ma; Coxall et al., 2005) and to the establishment of a climate state more similar to the modern. On the whole, the very warm early Eocene greenhouse climate lasted unabated for ~4 Myr (54–50 Ma; Inglis et al., 2015; Lauretano et al., 2015; Dallanave et al., 2016; Cramwinckel et al., 2018).

The late Paleocene and early Eocene were punctuated by transient episodes of climate instability generally attributed to carbon cycle perturbations and called hyperthermals. Hyperthermals had average durations of tens of thousands years, and were characterized by large temperature anomalies associated with negative carbon isotope excursions (e.g., D'Onofrio et al., 2016; Luciani et al., 2017; Westerhold et al., 2018; Thomas et al., 2018). The largest and most known hyperthermal is the Paleocene/Eocene Thermal Maximum (PETM, 55 Ma; Kennett and Stott, 1990), when Earth rapidly warmed of at least 5 to 8 °C globally (Pagani et al., 2014) with tropical sea surface temperatures possibly reaching or exceeding 40 °C (Aze et al., 2014).

Carbon cycle feedbacks involved in maintaining high temperatures and pCO₂ over millions of years and allowing periodical extemporaneous hyperthermals are unclear. Temperature-dependency of metabolic rates has been proposed to explain the Eocene high-

temperature and high-CO₂ climate (Olivarez-Lyle and Lyle, 2006). In agreement with Olivarez-Lyle and Lyle (2006), there is evidence for a much shallower organic matter remineralization depth in greenhouse climate oceans. Using stable isotopes measured on planktonic foraminifera, John et al. (2013, 2014) reconstructed Eocene δ¹³C dissolved inorganic carbon (DIC) profiles for the upper few hundred meters of the water column in Tanzania and Mexico. The basic idea was that rapid remineralization of organic matter to CO₂ through the upper part of the water column, caused by faster microbial respiration in warmer waters, would have caused steeper carbon isotope gradients than are typical today. The reconstructed gradients are indeed much steeper, consistent with the idea that the greater proportion of the organic matter was respired high in the water column (John et al., 2014, Figs. 1, 3). Using numerical model experiments Komar et al. (2013) suggested that both the long term Eocene warm climate and transient hyperthermals are best explained by a drop in net organic carbon burial. Similarly, Ma et al. (2014) reconstructed marine barite accumulation rates over the Paleocene/Eocene Thermal Maximum, and argued for a reduced carbon pump to deeper waters as expected from temperature-dependent microbial respiration rates. Inputs of light carbon into the ocean-atmosphere system in the form of CO₂ or CH₄ are generally considered the most likely trigger for hyperthermals. However, sources and triggers for such emissions are still strongly debated (Komar et al., 2013; Kirtland Turner et al., 2014; Ridgwell and Arndt, 2014; Gutjahr et al., 2017; Thomas et al., 2018). Temperature related changes in water column parameters may in turn have played a major role in controlling the evolution of plankton in the ocean. For instance, gradual deep-water cooling in the Eocene may have allowed progressively more organic matter to be exported below the euphotic zone, opening up new ecological niches for deep-dwelling, low oxygen tolerant microzooplankton (Pearson and Coxall, 2014). Global warming events during the Eocene, such as the Middle Eocene Climatic Optimum and the Eocene hyperthermals, appear in fact to have led to marked restructurings and possible partial collapse, of pelagic food webs, associated with a sharp decline in the export of organic carbon and with benthos starvation (Boscolo-Galazzo et al., 2014, 2015; Thomas et al., 2018; Jennions et al., 2015). Major Phanerozoic extinction/speciation events may be imputable to climate change via temperature-dependent restructuring of marine biological communities (Stanley, 2010; Meyer et al., 2016).

Stanley (2010) suggested that the coupling between oxygen and carbon isotope trends in marine carbonates of the entire Phanerozoic (last 540 Ma) could be controlled largely by temperature-dependent variations in global organic carbon burial rates. In this scenario, cool climates with relatively positive δ¹⁸O recorded in carbonate fossils tend to result in more efficient burial of isotopically light carbon, leaving the residual ocean DIC enriched in δ¹³C, and vice-versa. If Stanley is correct then temperature-dependent metabolic processes are one of the defining features of Earth's environmental history. However it should be noted that there are other reasons why oxygen and carbon isotope ratios in marine carbonates may co-vary, for instance by the exchange of isotopically light carbon between buried methane and the atmosphere.

6. Conclusion

Temperature-dependent processes controlling deep sea carbon fluxes (Figs. 2, 3, 4) are likely to impact both the cycling of carbon in the ocean-atmosphere system and the long-term burial-weathering cycle, with the potential to regulate atmospheric CO₂ and Earth temperature over multi-millennial time scales (Olivarez-Lyle and Lyle, 2006; Roth et al., 2014; John et al., 2014). We propose that the Earth system may be equipped with two independent thermostats ultimately linked by atmospheric concentrations of CO₂: the abiotic chemical weathering thermostat (Bernier and Caldeira, 1997) and the metabolic thermostat, controlled by the effects of temperature on the biological cycling of carbon (Fig. 4) (which could be on land, as well as in the ocean).

The real-world processes are undoubtedly complex and spatially variable. In a changing climate there will be multiple interactions with other aspects of ocean biology, chemistry and structure, including changes in the vertical distribution of plankton communities with linkages to other environmental drivers such as ocean deoxygenation, stratification and acidification. Although recent research has pointed the way forward on many of the key interactions, they remain poorly understood, as does their interplay over different timescales. To better understand this complexity we need more empirical data on biological pump efficiency from the modern ocean (e.g., with changing phytoplankton composition, grazing pressure and oxygen concentrations) as well as palaeo data from both warm and cold climate states in Earth's past (e.g., new, integrated approaches to investigate the efficiency of the biological pump in the past and over geological time, proxies for nutrient regeneration), a sounder modelling framework (e.g., improved parameterization of remineralization and biogeochemistry), together with a better integration among these different fields of research.

Acknowledgments

FBG and KAC was supported by Natural Environmental Research Council (NERC) grant number 01633400765 to PNP and SB. FBG thanks E. Fornaciari for fruitful discussions. The authors acknowledge two anonymous reviewers and the Editor T. M. Cronin for their helpful feedback that significantly improved the paper.

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